

# Tropical mycorrhizas, nutrient cycles and plant growth

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## SUMMARY

1 Most rain forest tree species form vesicular-arbuscular mycorrhizas (VAM). Only a few species from several unrelated plant families form ectomycorrhizas (EM) in the tropics, although those that do are often locally abundant as colonizing species or forest dominants.

2 Both VAM and EM improve the uptake of mineral nutrients, especially immobile ones such as phosphorus, with their extensive, well-distributed mycelia. In addition, the mycorrhizal fungi of orchids and some EM fungi may directly recycle nutrients from litter by decomposing it. VAM fungi are unlikely to do so.

3 Mycorrhizal fungi almost completely close tropical mineral cycles by their efficient uptake of mineral nutrients from the soil, their advantageous position for scavenging mineral nutrients from dying roots, and their possible interspecific transfer of mineral nutrients.

4 VAM have been shown to improve the growth and survival of several tropical plants; only two indigenous rain forest tree species have been tested for response to EM, both of which showed improved growth. Species are facultatively or obligately dependent on VAM or EM for mineral nutrient uptake and growth, or are non-mycorrhizal.

5 Different dependencies on VAM or EM are adaptations to different soil fertilities and probabilities of mycorrhizal infection: EM species are favoured by seasonal dryness, inhibited nitrification, and extremely low mineral retention by soils such as white sands; facultatively mycotrophic species are favoured by high soil fertility; non-mycorrhizal species are favoured by slow rates of mycorrhiza formation by competing dependent species. Most mature-forest tree species are obligately mycotrophic.

6 Changes in soil fertility or in the probability of mycorrhizal infection can influence succession by favouring species with different dependencies on mycorrhizas. The probability of infection in rain forest soil can change markedly because these soils do not contain large numbers of spores.

7 EM species often dominate low-diversity tropical forests on poor soils because they have specific, highly-beneficial fungal associates. VAM hosts predominate in forests with moderate turnover rates on soils of intermediate fertility; their dependence on the same few mycorrhizal fungus species for mineral nutrient uptake limits their ability to competitively exclude one another, and thereby contributes to high within-habitat species diversity.

## INTRODUCTION

In his comprehensive account of tropical rain forest, Richards (1952) noted that mycorrhizas might predominate among rain forest plants, but that little could be said with certainty about their ecological significance. Since that statement, sufficient data have accumulated to conclude that mycorrhizas are ubiquitous and important for the mineral nutrition, growth, and survival of lowland tropical plants, although knowledge of the role of mycorrhizas in tropical ecosystems is far from complete. In this paper I review the occurrence of mycorrhizas in the lowland humid tropics, their potential role in nutrient cycling, effects on plant growth, and possible influence on species composition of lowland humid tropical plant communities.

## TYPES OF MYCORRHIZAS

Most tree species that are mycorrhizal have vesicular-arbuscular mycorrhizas, although some have ectomycorrhizas. This paper is mainly concerned with woody species and these two types of mycorrhizas. Orchid mycorrhizas (Lewis 1975) are abundant in the lowland tropics, but are considered here only with respect to nutrient cycles. Mycorrhizal types are distinguished on the bases of the taxonomic position of host and fungus, morphology, and anatomy; clear distinction between types is critical to understanding their different ecological roles.

*Vesicular-arbuscular mycorrhizas*

Almost all plants are capable of forming vesicular-arbuscular mycorrhizas (VAM) with fungi in a single zygomycetous family, the Endogonaceae (Gerdemann 1968). The submerged roots of aquatics usually are not infected, but some tropical freshwater (Bagyaraj, Manjunath & Patil, 1979), temperate swamp (Keeley 1980) and salt-marsh (see Gerdemann 1968) species can be mycorrhizal. I know of no published examinations of tropical swamp or mangrove species for mycorrhizas.

At present, over sixty species of VAM fungi have been described (see Hall & Fish 1979) in four genera (Gerdemann & Trappe 1974). Many are cosmopolitan, but some may be strictly tropical, e.g. *Acaulospora foveata* and *A. tuberculata* (Janos & Trappe 1982). The spores produced by VAM fungi are large and not wind-dispersed, although they may be moved with soil transported by wind or water. Earthworms, ants, wasps, and birds (McIlveen & Cole 1976) can transport spores with soil, but because of the low numbers of spores in tropical soils, (Janos 1980a), and the small amounts of soil carried, these are insignificant vectors. Rodents may be the principal long-distance vectors of VAM fungi (Maser, Trappe & Nussbaum 1978): spores have been found in faecal samples from Peru (L. H. Emmons 1982), and as stomach contents in the Galapagos (D. A. Clark, pers. comm.).

Most VAM infection in tropical rain forest is transmitted from root to root. This is possible in species-rich forests because VAM fungi have virtually unrestricted host ranges (Janos 1980b). The fungi cannot grow if unassociated with host roots

(Gerdemann 1968); broad host ranges compensate for poor dispersal. VAM fungal species differ in effectiveness—the extent to which they stimulate host growth (Mosse 1973)—because of different abilities to grow in different soils (Lambert, Cole and Baker 1980). Fungal species in the VAM genus *Acaulospora*, for example, seem adapted to acid soils (Nicolson & Schenck 1979).

Although VAM are morphologically similar to uninfected roots, the characteristic anatomical structures responsible for their name (see Mosse 1959; Nicolson 1959; Gerdemann 1968) are revealed by decolourizing and staining whole, young, unsterilized, corticated roots (Phillips & Hayman 1970). Vesicles or the more ephemeral arbuscules must be observed to document VAM occurrence, even though typical dimorphic VAM fungus hyphae may be seen by microscopic examination of root surfaces. Much external mycelium is lost when roots are extracted from the soil.

Bowen (1980) recently reviewed how mycorrhizas function. Both VAM and ectomycorrhizal fungi enhance the supply of several mineral nutrients to their host; carbon compounds pass from host to fungus. Enhanced nutrient uptake, especially of poorly mobile ions such as phosphate, is attributable to the extensive, well-distributed absorbing surface provided by mycelium external to the root. VAM fungi take up phosphorus from the same pool of soluble phosphate that is utilized by uninfected plants (Mosse 1973), but exploit a larger volume of soil than do roots (Owusu-Bennoah & Wild 1980). This seems to be the basis for uptake of slowly exchangeable soil phosphate (Owusu-Bennoah & Wild 1980) and sparingly soluble fertilizers (Mosse & Hayman 1980), although data of Höweler, Edwards & Asher (1981) suggest that hyphae are able to absorb phosphorus from lower concentrations than can uninfected roots. VAM fungi produce phosphatases (Macdonald & Lewis 1978) that allow utilization of organic phosphorus, especially under humid tropical conditions where hyphae can be in close contact with finely divided litter, and where acid soil reaction reduces the sorption of organic phosphates on soil surfaces (see Tinker 1975). Enhancement of nitrogen uptake by VAM is unlikely because nitrogen is highly mobile in soil solution and can freely diffuse to roots. VAM can have other effects on hosts, such as improved wilt-resistance (Safir, Boyer & Gerdemann 1972) or disease resistance (Daft & Okusanya 1973), but these may result secondarily from improved host mineral nutrition.

#### *Ectomycorrhizas*

In the lowland humid tropics, ectomycorrhizas (EM) are a regular feature of Dipterocarpaceae, Fagaceae and Pinaceae, and have been reported for species of several genera of Caesalpinoideae (Janos 1980a; Redhead 1980). In addition, EM have been observed by at least two investigators at different sites on species of Euphorbiaceae (*Uapaca*: Horak 1977; Redhead 1980), Gnetaceae (*Gnetum*: Horak 1977; St John 1980a), Myrtaceae (*Campomanesia*: Thomazini 1974; *Eucalyptus*: Horak 1977; *Eugenia*: Shamsuddin 1979; *Melaleuca*: Horak 1977), Nyctaginaceae (*Neea*: Janos 1980a; St John 1980a; *Pisonia*: Pegler & Fiard 1979), Papilionoideae (*Ormosia*: Edmisten 1970; St John & Uhl 1983), Polygonaceae (*Coccoloba*: Kreisel 1971; Janos 1980a) and Sapindaceae (*Allophylus*: Singer & Morello 1960; *Nephelium*: Alexander

1981). The EM habit seems to have evolved several times, often with species of groups noted for the production of resins or polyphenols that might control the spread of fungal associates within the root (see Marks & Foster 1973).

Native lowland tropical EM fungi are predominantly Basidiomycetes (Singh 1966; Horak 1977; Singer & Araujo 1979; Ivory 1980), although Ascomycetes are also involved (*Cenococcum* sp.: de Alwis & Abeynayake 1980). On a worldwide basis, EM fungal species number in the thousands (Trappe & Fogel 1977), but because of the paucity of EM hosts and investigations of them, few tropical species have been reported. Some tropical EM fungal species, such as the rough-spored boletes reported to associate with dipterocarps (Malloch, Pirozynski & Raven 1980), are holarctic; others are strictly tropical (Horak 1977). Most Basidiomycetes produce numerous small, wind-dispersed, spores which are broadly distributed. Restriction of species to the tropics probably resulted from adaptation to specific site factors such as high soil temperatures or high moisture regimes (see Bowen & Theodorou 1973), or from host specificity. Many species of EM fungi associate with a single genus or subgenus of host (Trappe & Fogel 1977); others such as *Cenococcum* spp. and *Pisolithus tinctorius* (Pers.) Coker & Couch (Marx 1977) have broad host ranges. Redhead (1980) found that the indigenous EM fungi of two Nigerian caesalpinoid legumes would not form mycorrhizas with an introduced pine, nor would an EM fungus of pine produce mycorrhizas on the legumes.

The distinguishing features of an EM are a fungal mantle of septate hyphae ensheathing the root, and a Hartig net composed of hyphae which penetrate between and surround the cortical cells. Intracellular penetration of cortical cells is uncommon, but can develop as roots age (Alexander & Hardy 1981) or in association with 'virulent' fungi (Norkrans 1950). Hyphae, and/or mycelial strands or rhizomorphs extend from the EM. In addition, the absorptive surface of EM roots *per se* is increased by their large diameter, many branches and the mantle.

EM, like VAM, improve the uptake of immobile mineral nutrients principally by extensive exploitation of the soil (Bowen 1980). Moreover, the EM mantle can buffer hosts against fluctuations in phosphorus supply by storing phosphorus when it is readily available and later releasing it to the host when exogenous availability is low (Harley & Lewis 1969). EM fungi produce phosphatase (Alexander & Hardy 1981), and can utilize organic phosphorus subject to the same constraints as VAM fungi. Some EM fungi excrete oxalate which is thought to increase the availability of organic phosphorus and nitrogen by releasing organic material from aggregation with minerals (Graustein, Cromack & Sollins 1977). Simple organic nitrogen compounds such as amino acids are utilized by EM fungi, although ammonium is probably their primary nitrogen source in nature (Alexander 1983). EM supply water to hosts (Duddridge, Malibari & Read 1980), and protect feeder roots from disease (Marx 1972).

#### OCCURRENCE OF MYCORRHIZAS

Surveys of tropical forest indicate that the absence of mycorrhizas is exceptional. Janse (1896) sampled plants at the periphery of a mid-elevation forest in Java, and found

that all forty-six arborescent species examined had VAM. Of a total of seventy-five species from fifty-six families, he found only six herbaceous species lacked mycorrhizas. Johnston (1949) observed VAM in all thirteen forest tree species he surveyed in Trinidad, including some of the most common species on the island. Of his total of ninety-three species from several different habitats only thirteen were uninfected. Redhead (1968) looked at sixty-six species from twenty-five families in Nigeria; of these, fifty-one species were indigenous to lowland rain forest, and of the indigenous species, three had EM, and forty-four had VAM (Redhead 1980). Only very young plants or those from newly cleared and burnt nurseries lacked mycorrhizas. Shamsuddin (1979) reported that of about 200 species of Malaysian forest trees, only one lacked mycorrhizas. All forty species of Dipterocarpaceae examined, and some Pinaceae, Fagaceae and Myrtaceae had EM. In Sri Lanka, de Alwis & Abeynayake (1980) observed mycorrhizas on fifty-nine of sixty-three species belonging to twenty-six families. The five dipterocarp species examined had EM. St John & Uhl (1983) found all twelve forest and ten early-successional species that they examined from seventeen families to be mycorrhizal; three leguminous species had EM. An extensive survey conducted by St John (1980a) near Manaus, Brazil, however, stands in opposition to these other studies. He found three tree species out of eighty-six from thirty-seven families with EM, which agrees with the low numbers of EM species usually encountered, but did not observe mycorrhizas on twenty-five species.

Other data are either not from collections made in forest or are difficult to interpret, but accord with the prevalence of VAM on lowland tropical trees. Janos (1980b) inoculated seedlings of twenty-three tree species from fourteen families in Costa Rica with VAM fungi, and noted that all formed mycorrhizas. St John (1980b) listed sixty-four VAM species, including many of economic importance, from several habitats in Brazil other than the primary forest in his aforementioned study (St John 1980a). Thomazini (1974) observed that all sixty species she collected from Brazilian *cerrado* had mycorrhizas, but listed the majority of species as having 'endotrophic mycorrhizae with septate mycelia'. Her description implies mycorrhizas with ericaceous or orchidaceous affinities (see Lewis 1975), although VAM mycelia may become irregularly septate with age and many of the genera she lists are known to form VAM. She found two species had EM. Edmisten (1970) failed to find mycorrhizas in nine of thirty-two principal forest species in Puerto Rico; however, his results probably reflect the difficulty of observing VAM in sectioned roots. He listed six species as EM, but three of these are unusual records requiring independent confirmation.

Reports of EM from the lowland humid tropics are seldom well-documented, and some may be unreliable. Descriptions and photomicrographs of sectioned EM roots of native tropical species have rarely been published. Sections are needed because non-mutualistic fungi can form mantle-like structures giving the superficial appearance of EM (Levisohn 1954a). Some authors (e.g. Pegler & Fiard 1979) have listed plant species as EM apparently without root examination, because of proximity to a fungus fruiting-body in a genus thought to be obligately EM. Nevertheless, the families previously listed can be considered to contain EM species because of multiple, independent records.

Where EM species do occur in rain forest they are often locally abundant or clumped, either as (i) pioneer or gap-colonizing species (*Allophylus*: Singer & Morello 1960; *Neea*: Janos 1980a), or (ii) dominants of mature communities (*Coccoloba*: Kreisel 1971; *Aldinia*: Singer & Araujo 1979; *Eugenia*: Shamsuddin 1979; *Brachystegia*: Redhead 1980; *Caesalpinioideae*, *Dipterocarpoideae*, *Fagaceae*: Malloch, Pirozynski & Raven 1980; Janos 1980a). Janos (1980a) suggested that EM species are effective colonizers because their wind-dispersed fungus associates may invade disturbed areas more quickly than VAM fungi. Baylis (1975) speculated that a specific EM association might favour the competitive ability of a host species and promote its abundance.

Some tropical species can form both EM and VAM (*Hopea*: Shamsuddin 1979; *Glycoxylon inophyllum* (Mart. ex Miq.) Ducke: reported to have VAM by St John 1980b, and EM by Singer & Araujo 1979; *Casuarina*: National Research Council 1982a; *Eperua purpurea* Benth.: St John & Uhl 1983), an ability reported for only five genera of temperate zone trees (Levisohn 1954b; Vozzo & Hacskeylo 1974; Baylis 1975). Study of such species could reveal the relative ecological costs and benefits of VAM and EM. Vozzo & Hacskeylo (1974) noted a *Populus* species that normally formed EM had only VAM when growing in fertile flood-plain soil. Baylis (1975) observed a normally VAM myrtaceous species that had EM when growing in pure stands. Simultaneous VAM and EM infections of the same root tip have been observed (*Leptospermum*: Baylis 1962), but it is not known if either infection is mutualistic in such cases. Little is known of the physical or chemical constraints that result in the usual fidelity of host species to one mycorrhiza type.

#### ARE TROPICAL MINERAL NUTRIENT CYCLES DIRECT?

Richards (1952) predicted that rain forest nutrient cycles should be almost completely closed, minimizing mineral losses, because nutrient influx to these ecosystems is limited. The idea that mycorrhizal fungi might effect such closure by decomposing litter and transporting the mineral nutrients thereby released to their hosts is attractive; Went & Stark (1968a, b) proposed this idea as a 'direct mineral cycling' hypothesis. Although not conclusively demonstrated, direct nutrient cycling is presented as a property of tropical rain forests by several general texts (e.g. Farnworth & Golley 1973; Walter 1973; Smith 1980; National Research Council 1982b).

Demonstration of direct nutrient cycling has been confounded by imprecise definition, and especially by failure to properly distinguish between the potential involvement of VAM and EM. Closure of tropical mineral nutrient cycles can result from retention of mineral nutrients by superficial mats of roots and humus (Herrera *et al.* 1978a), and this phenomenon may be confused with direct nutrient cycling in the strict sense. Stark & Jordan (1978) demonstrated that such a root mat retained virtually all of the radioactive calcium and phosphorus solution they applied, but retention was attributed to rapid surface adsorption by organic material rather than to absorption by roots (Herrera *et al.* 1978a).

Direct nutrient cycling requires that mycorrhizal fungi decompose organic material. Orchid mycorrhizal fungi acquire carbon as decomposers (Lewis 1975), and



transfer it to heterotrophic orchid protocorms. Hutchison (1981) demonstrated that orchid mycorrhizas supply other elements to mature orchids. Thus, orchids probably cycle minerals directly, but orchid mycorrhizas are distinct from other mycorrhiza types. Potential involvement of tree mycorrhizas in direct nutrient cycling is suggested by data of Herrera *et al.* (1978b) who showed that radioactive phosphorus was present in a mycorrhizal fungus hypha and the living root that it connected to a dead leaf labelled with the isotope. One cannot be sure, however, that the isotope was transported to the root through the hypha, or if the mycorrhizal fungus itself was responsible for release of the isotope from cells of the dead leaf. The directness of terrestrial mineral nutrient cycles can only be resolved by demonstration of enzymatic capability of VAM or EM fungi to mineralize litter.

#### *Decomposition by mycorrhizal fungi*

The ability of VAM and EM fungi to digest cellulose and lignin in the soil when associated with a host is unknown, but available data suggest that some EM fungi break down these compounds. There is little unequivocal evidence for either the ability or inability of VAM fungi to degrade these substances, although they seem less likely than EM fungi to have decomposing capability.

An EM was almost certainly involved in the observations of Herrera *et al.* (1978b) that hint at direct mineral cycling (Singer & Araujo 1979). Evidence is scant, however, for decomposition of organic materials by EM fungi associated with a host. Todd (1979) reported that five common temperate zone EM fungi in axenic culture with a host could break down hemicellulose, cellulose, litter and a model humic polymer labelled with radioactive carbon, as evidenced by the evolution of labelled carbon dioxide. Unfortunately, he published only an abstract, making evaluation of his observations difficult. In contrast, Thomas *et al.* (1982) found that seedlings with another EM fungus did not utilize more non-labile phosphorus than uninfected control seedlings.

Data on the ability of EM fungi to produce cellulolytic or lignin-degrading enzymes are conflicting. Most studies have involved pure cultures of fungi, and the mutualistic nature of those isolates that could grow on cellulose or degrade complex phenolics has been questioned. If the source of an isolate was a fruit-body and not a mycorrhizal root, the isolate might be a non-mycorrhizal strain. Moreover, simple soluble sugars contaminating media might cause apparent growth on complex substrates, leading to erroneous inference of decomposing ability. Despite such reservations, Hacskeylo (1973) and Trappe & Fogel (1977) concluded that although the majority of EM fungi seem to have little or no ability to break down complex carbon compounds, some species do. Recently, Giltrap & Lewis, (1981) suggested that some of the earlier reports of failure of EM fungi to grow on complex carbohydrates reflected growth inhibition by phosphate, rather than inability to degrade a complex substrate. Production of lignin-degrading polyphenol oxidases by some EM fungi has been confirmed (Giltrap 1982). The only report of successfully cultured indigenous tropical EM fungi did not include tests of cellulase or polyphenol oxidase production (de Alwis & Abeynayake 1980).

Some EM fungal species can exist as saprophytes in nature (Lewis 1975). Singer (1971) and Hacskeylo & Bruchet (1972) have observed two EM fungal species fruiting in the absence of hosts, suggesting that these strains are saprophytic. Norkrans (1950) showed that a fungus producing cellulase and growing on cellulose in culture, could form EM and ectendomycorrhizas. She hypothesized that glucose supplied to the fungus by a host could suppress cellulase production resulting in a stable mutualism. Giltrap & Lewis (1982) confirmed that synthesis of pectin-degrading enzymes by an EM fungus in pure culture could be repressed by large amounts of glucose. Small amounts of 'starter' glucose, however, can greatly facilitate the induction of pectin-degrading enzymes and utilization of cellulose as a carbon source by some EM fungi in pure culture (Giltrap & Lewis 1982; Norkrans 1950). Mycorrhizal fungi with such inducible enzymes, although ineffective competitors with other soil micro-organisms as saprophytes, and unable to live apart from their hosts, might be able to decompose litter when associated with a host. All evidence considered, it seems likely that there are EM fungus species with some saprophytic ability.

VAM fungi are less likely than EM fungi to decompose litter, although some authors imply that VAM fungi have this ability. Ultrastructural studies suggest that penetration of host roots by VAM fungi is not completely physical. The fungi seem to produce enzymes that loosen the fibrillar structure of the host cell wall, at least locally at hyphal tips (Holley & Peterson 1979). Mosse (1959) anecdotally remarked that VAM fungi appeared to accelerate the breakdown of organic matter. Nevertheless, she acceded that accelerated breakdown of organic matter could be an indirect effect of the presence of VAM fungi, for example, by stimulation of other micro-organisms (e.g. Barea, Azcon & Hayman 1975). Warner & Mosse (1980) felt that their data on spread of VAM fungi through soil in the absence of a host indicated saprophytic ability, but the fungi produced numerous, small secondarily-formed, 'vegetative spores' which could have caused the observed spread if infective.

The anatomy, phosphorus utilization pattern, and ubiquity of VAM imply that VAM fungi lack decomposing ability. No points of hyphal egress from living roots suggestive of exploitation of external carbon sources have been observed; infection spreads within roots away from penetration points (Mosse 1959; Nicolson 1959). Moreover, in several soils mixed with 25% peat, the one VAM fungal species tested utilized the same pool of soluble phosphorus as uninfected roots (Hayman & Mosse 1972). Similar results, however, were obtained with the sole EM fungal species tested in a comparable manner (Thomas *et al.* 1982). VAM fungi associate with a tremendous range of host-plants including most herbs; EM are formed by relatively few taxa of which very few are herbs (e.g. Fontana 1977). VAM fungi probably would not be so ubiquitous if they produced significant amounts of cellulase and were thereby more expensive of energy for hosts to control.

#### *Closure of mineral nutrient cycles*

Direct nutrient cycling is probably neither a general tropical phenomenon, nor an ecosystem-wide phenomenon. Rather, it is likely to be a property of orchid species and



some EM trees. EM tree species can be locally abundant on extremely poor sites in the lowland tropics, such as those with Spodosols (Singer & Araujo 1979), for which direct nutrient cycling was originally hypothesized. Spodosols, however, constitute only 1% of the world's lowland humid tropical soils (National Research Council 1982b).

Closed mineral nutrient cycles that do not require decomposing ability of mycorrhizal fungi can be widespread. Root mats characterize some ecosystems (Herrera *et al.* 1978a) and single species (e.g. *Oenocarpus panamanus* Bailey: pers. observation). Whittingham & Read (1982) demonstrated that VAM fungi connecting individuals of different species could transport phosphorus from one to another. Reid & Woods (1969) inferred that EM fungi could similarly transport substances between conspecific individuals. If significant quantities of mineral nutrients become available to mycorrhizal fungi as host roots senesce, then such interconnections close mineral cycles.

There is little doubt that mycorrhizas are important for achieving almost complete closure of tropical mineral nutrient cycles for some elements such as phosphorus. Mycorrhizas are efficient at uptake from the soil solution to which mineral nutrients are added by precipitation (Kellman, Hudson & Sanmugadas 1982), throughfall, and stemflow (McColl 1970). Root turnover can be rapid in tropical forests (Jordan & Escalante 1980), and although production of above-ground biomass much exceeds root production per annum, root death may contribute a significant portion of the annual organic matter input to the soil (see Alexander 1983). By virtue of their position, mycorrhizal fungi associated with dying roots could be effective in scavenging nutrients from them in competition with other soil micro-organisms (Heap & Newman 1980), even though dependent on the exoenzymes of other micro-organisms for mineralization.

#### EFFECTS ON PLANT GROWTH

Because mycorrhizas increase mineral nutrient uptake from infertile or nutritionally imbalanced soils, VAM have often been observed to improve the growth of annual crops, and EM to benefit seedlings of temperate zone timber tree species. Improvements in growth of lowland tropical species have been obtained primarily with VAM on economically important species: *Citrus* varieties (Marx, Bryan & Campbell 1971), pasture legumes (*Centrosema*, *Lotus*, *Stylosanthes*: Crush 1974; *Leucaena*: Yost & Fox 1979; *Calopogon*, *Desmodium*, *Pueraria*: Waidyanatha 1980), pasture grasses (*Paspalum*: Mosse 1972; *Brachearia*: Mosse 1975; *Agrostis*: Pichot & Truong 1980), field crops (*Arachis*: Daft & El-Giahmi 1976; *Oryza*: Sanni 1976a; *Vigna*: Sanni 1976b; *Manihot*: Yost & Fox 1979; *Eupatorium*, *Guizotia*, *Tagetes*: Moawad 1980), fruits (*Carica*: Ramirez, Mitchell & Schenck 1975; *Litchi*: Pandey & Misra 1975; *Bactris*: Janos 1977; *Persea*: Menge *et al.* 1978; *Piper*: Krikun & Bar Joseph 1979; *Psidium*, *Solanum*: Janos 1980b), and ornamental or timber trees (*Acacia*: Johnson & Michelini 1975; *Khaya*: Redhead 1975; *Vitex*: Janos 1975a; *Pentaclethra*, *Terminalia*, *Virola*: Janos 1980b; *Enterolobium*: McHargue 1981). Formation of VAM is a prerequisite for nodulation of many legumes by nitrogen-fixing bacteria (Mosse 1977; Janos 1980b; McHargue 1981). Indigenous tropical EM fungi improved the growth of *Brachystegia eurycoma*

Harms, a common mature-forest tree in Nigeria (Redhead 1980), and *Neea laetevirens* Standl., a small tree of second-growth vegetation in Costa Rica (D. P. Janos, unpubl. data). Additional data on the growth effects of indigenous tropical EM fungi are lacking, however, which is surprising in view of the economic importance of the Dipterocarpaceae.

Experiments to demonstrate effects of mycorrhizas on growth usually are conducted in pots of sterilized soil, but field (see Mosse & Hayman 1980) and nursery (see Mikola 1973) studies have shown similar effects. Cautious qualitative extrapolation from plant responses in limited volumes of soil to anticipated responses in the field is justified. VAM inoculation can improve plant growth in unsterilized fields (Mosse & Hayman 1980) by accelerating mycorrhiza formation or by introducing strains that are more effective than indigenous fungi. Pines cannot be grown where they are not native unless inoculated with EM fungi (Mikola 1973). VAM inoculation has improved seed yields of annual crops (see Khan 1975; Sanni 1976a), and VAM and EM have improved fruit and timber tree seedling survival (e.g. Janos 1977, 1980b; Menge *et al.* 1978; Trappe & Strand 1969). Thus, mycorrhizas may have the ability to influence the ecological fitness of plant species in natural vegetation.

#### *Degrees of dependence on mycorrhizas*

In a series of pot experiments with seedlings of thirty-two species of lowland tropical plants, Janos (1975a, 1977, 1980b) found that VAM improved the growth of twenty-eight species, including all of the mature-forest tree species, but that the species differed in their degree of dependence on VAM. Some were able to grow without mycorrhizas, although mycorrhizas improved their growth, while other species could neither grow nor survive without mycorrhizas. The former are facultatively mycotrophic; the latter, if unable to grow without mycorrhizas in the most fertile of their natural habitats, are ecologically obligately mycotrophic. EM species may be ranked along this same continuum. *Neea laetevirens* is facultatively dependent on EM; seedlings grew best when fertilized with ashes at a rate equivalent to that produced by land clearing, although the number of mycorrhizas per seedling decreased with fertilization (D. P. Janos, unpubl. data). Uninoculated *Pinus caribaea* Morelet did not respond to fertilizer applications (Vozzo & Hacskeylo 1971), suggesting obligate dependence on mycorrhizas.

Facultative mycotrophs probably are superior competitors to other species on fertile soils; obligately mycotrophic species are likely to be the best competitors under infertile conditions provided that mycorrhizas form (Janos 1980a). In fertile soil, facultatively mycotrophic species reject mycorrhizas which are of no benefit for mineral nutrient uptake and would exact a potentially detrimental energy cost (Bowen 1980). Their independence of mycorrhizas is correlated with fine roots and profuse root hairs (Baylis 1975; St John 1980c). Obligate mycotrophs have coarse, hairless roots, and are less subject than facultative mycotrophs to wounding and pathogenic infection, and to the potential disadvantages in infertile soil of greatly-overlapping mineral depletion zones (Tinker 1975) and rapid root-system turnover.

Several additional factors are correlated with independence of mycorrhizas.

Facultative mycotrophs may root more deeply (St John 1980a), produce greater root biomass, have higher root/shoot ratios (Azcón & Ocampo 1981), or have lower total mineral requirements (see Janos 1980b) than obligate mycotrophs. Growth rate (Janos 1975b) and tissue mineral concentration (Azcón & Ocampo 1981), however, need not be correlated with independence of mycorrhizas.

Tropical tree species that are strongly dependent on mycorrhizas often have large seeds (Janos 1980b) which favour the persistence of uninfected seedlings and the formation of large pre-infection root systems, maximizing the probability of infection. Obligate mycotrophs are often light-demanding, in part because of the energy requirements of mycorrhizal association. Of two co-occurring *Shorea* species (Dipterocarpaceae) in Malaysia, the species with the higher proportion of infected seedlings and the greater number of EM per infected seedling had the lower rate of seedling survival in forest understorey (P. Becker, pers. comm.). Mycorrhizas—a liability in shade—may have been sustained because of their importance to immediate, rapid seedling growth when canopy gaps open. Mature forest canopy and sub-canopy tree species tend to be obligately mycotrophic; many pioneer and early successional species are facultatively mycotrophic or non-mycorrhizal (Janos 1980b).

Species of Aizoaceae, Amaranthaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Commelinaceae, Cyperaceae, Fumariaceae, Juncaceae, Nyctaginaceae, Phytolaccaceae, Polygonaceae, Portulacaceae, and Urticaceae usually do not form mycorrhizas (Gerdemann 1968), although VAM stimulated the growth of a chenopod (Williams, Wollum & Aldon 1974), and EM benefited the nyctaginaceous *Neea laetevirens*. Many species of Proteaceae in the genera *Hakea* (Lamont 1972), *Banksia* and *Personia* (Khan 1978) also are non-mycorrhizal, but species of other proteaceous genera have VAM (*Grevillea*: Bakshi 1974; *Helicia*: Janse 1896; *Roupala*: Thomazini 1974). In addition, some species of other families such as the Lecythidaceae (St John 1980a) and Sapotaceae (St John 1980a; de Alwis & Abeynayake 1980) may be non-mycorrhizal. *Ananas comosus* (L.) Merr. (Maeda 1954), *Areca catechu* L. (de Alwis & Abeynayake 1980), and *Durio zibethinus* Murr. (Shamsuddin 1979) are economically important tropical species that have been examined for mycorrhizas and found to lack them, although other members of the families of the latter two species are known to have VAM. Non-dependence on mycorrhizas needs to be confirmed by growth experiments.

Non-mycorrhizal species are not dependent on mycorrhizas even under infertile conditions because, like facultative mycotrophs, they have fine, highly-branched roots, numerous root hairs, or low tissue mineral requirements. *Hakea*, *Banksia* and *Personia* species produce dense clusters of rootlets on what are known as 'proteoid' roots. In addition, non-mycorrhizal species may liberate bound organic phosphorus by secreting organic acids (see Tinker 1975 and Graustein, Cromack & Sollins 1977), or have slow growth rates or durable tissues that compensate for limited nutrient supply. Non-mycorrhizal species actively reject mycorrhizal association because it is incompatible with their physiology, or in order to favour their persistence in competition with mycotrophic species (Janos 1980b). They are the only species that are effective competitors on infertile soils in the absence of mycorrhizal fungi.

Mineral nutrient availability (especially that of phosphorus), and the probability of mycorrhizal infection in different habitats (Janos 1980a) are probably the primary selective factors that produced different dependencies on mycorrhizas. In addition to the probability of infection, the factors most likely to influence the type of mycorrhiza upon which a host depends are seasonal dryness, periodic mineral nutrient availability, the form in which nitrogen is available, and suppression of decomposition by toxic compounds in litter or by low C/N ratio (see Janos 1980a).

Dependence on mycorrhizas influences, and is probably influenced by the dispersion characteristics and demography of plant species. For example, clumped or locally abundant non-mycorrhizal and EM species are likely to create conditions that favour their continued success: non-mycorrhizal species lower soil infectiveness; EM species increase infectiveness with respect to specific fungus associates (Janos 1980a). Non-mycorrhizal species and some EM species can have the demographic characteristics of pioneer or fugitive species because non-mycorrhizal plants can quickly establish without awaiting infection, and EM inoculum can build up very rapidly. Obligate mycotrophs probably are the best competitors under mature forest conditions; those with large seeds maximize the probability of seedling infection, and the continuance of mycorrhizal association is thereby favoured.

### COMMUNITY COMPOSITION

Dependence of plant species on different types of mycorrhizas to different extents can influence the composition of both seral and mature plant communities. Janos (1980a) described how obligate mycotrophs could replace non-mycorrhizal and facultatively mycotrophic seral species during tropical succession. Replacement is caused by declining fertility as soils age, or by increasing probability of mycorrhizal infection subsequent to a succession-initiating event that reduced or eliminated mycorrhizal fungus populations. Direct effects of mycorrhizas on succession depend upon changes in probability of infection that can occur when persistent, large populations of spores are not present. Humid-tropical soils under native vegetation (Redhead 1977; Herrera & Ferrer 1980; Janos 1980a; St John & Uhl 1983), a tree nursery (Redhead 1977) and some tree plantations (Nadarajah 1980) usually contain few spores, although Waidyanatha (1980) found very many spores in rubber plantations. Spore numbers may decline rapidly if sporulation is infrequent, because spores germinate in the absence of hosts (Koske 1981) and are subject to predation and parasitism (Redhead 1977; Janos 1980a; Nadarajah 1980).

Mycorrhizal fungus population sizes are likely to be affected by plant community composition (Janos 1980a; Kormanik, Bryan & Schultz 1980), and, in turn, to influence it (Reeves *et al.* 1979; Shamsuddin 1980). Rapid mycorrhizal infection in a moderately fertile soil, for example, can allow an obligately mycotrophic seedling to outcompete a facultatively mycotrophic one which would otherwise outgrow it. VAM increased seedling survival of three strongly mycorrhiza-dependent tropical tree species in mixed plots of nine competing species that included non-mycorrhizal and facultatively mycotrophic ones (D. P. Janos, unpubl. data). These experiments also

suggested that VAM reduce differences in competitive ability among all species at typical tropical soil fertilities, and thereby contribute to the high within-habitat species diversity characteristic of most tropical forests.

Species diversity in mature tropical forests is correlated with the presence of different types of mycorrhizas. Several of the genera that contain species occurring in monospecific stands in the tropics (Connell 1978) are known to include EM members. Perhaps, as Baylis (1975) suggested, optimal EM associations assist a species to dominance. Monospecific stands are frequently found on infertile white sands (Richards 1952) where decomposing ability of EM fungi would be highly advantageous. Hosts associated with EM fungi with decomposing ability are unlikely to be abundant on fertile soils, however, because of carbohydrate and defensive costs associated with controlling the fungi. On relatively fertile soils VAM species are abundant; their diversity is high in part because of the inability of host species to rapidly outcompete one another when depending on the same fungus species for mineral nutrient uptake. The hosts of EM fungi without decomposing ability are effective competitors with VAM species on fertile soils where nitrification is inhibited or water and phosphorus availability is seasonal (Janos 1980a). Niche differentiation between EM and VAM species probably contributes to very high diversity in mixed dipterocarp forest.

Forest composition with respect to mycorrhiza types and dependencies may be strongly influenced by forest turnover rates (Janos 1980a). Frequent or extensive disturbance can favour non-mycorrhizal or EM species that are effective colonizers. The presence of such species might, in turn, lower diversity by reducing VAM fungus populations and impeding the establishment of obligately mycotrophic VAM hosts. Because of differences in forest composition, productivity need not be highly correlated with fertility. Mycorrhizas, especially EM with decomposing ability, compensate for low soil nutrient availability; at high fertility, dominance by facultative mycotrophs might lead to incomplete resource exploitation and lower production than achieved by a mixed community at lower fertility. Mycorrhizas influence nutrient cycling, plant growth and productivity in tropical rain forest; they may influence species diversity as well. Species diversity is highest in rain forests with moderate turnover rates on soils intermediate in fertility between very nutrient-poor tropical white sands and rich, recent volcanics (see Huston 1980) perhaps because these conditions allow species of all degrees of dependence on both VAM and EM to coexist.

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